THE AVIAN CECUM: A REVIEW

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ABSTRACT.—The ceca, intestinal outpocketings of the gut, are described, classified by types, and their occurrence surveyed across the Order Aves. Correlation between cecal size and systematic position is weak except among closely related species. With many exceptions, herbivores and omnivores tend to have large ceca, insectivores and carnivores are variable, and piscivores and graminivores have small ceca. Although important progress has been made in recent years, especially through the use of wild birds under natural (or quasi-natural) conditions rather than studying domestic species in captivity, much remains to be learned about cecal functioning. Research on periodic changes in galliform and anseriform cecal size in response to dietary alterations is discussed. Studies demonstrating cellulose digestion and fermentation in ceca, and their utilization and absorption of water, nitrogenous compounds, and other nutrients are reviewed. We also note disease-causing organisms that may be found in ceca. The avian cecum is a multi-purpose organ, with the potential to act in many different ways—and depending on the species involved, its cecal morphology, and ecological conditions, cecal functioning can be efficient and vitally important to a bird's physiology, especially during periods of stress. *Received 14 Feb. 1994, accepted 2 June 1994.*

The digestive tract of most birds contains a pair of outpocketings that project from the proximal colon at its junction with the small intestine (Fig. 1). These ceca are usually fingerlike in shape, looking much like simple lateral extensions of the intestine, but some are complex in structure. Within the Class Aves, ceca range in size from very long to very short, or they may be entirely absent (Table 1). Unlike the case in almost all mammals, most avian ceca are paired and of approximately equal length, with separate lateral or ventrolateral openings into the colon (rectum). In some species the openings are dorsal or ventral, and a few paired ceca share a common orifice, but the great majority open into the lateral colon opposite one another (McLelland 1989). There has been confusion over how the passage of material through cecal openings is controlled, but it is now believed that the interdigitating meshwork of villi at the cecal entrance act as a filter, excluding large particles and allowing only fluid and fine particles to be separated and pushed from the colonic contents into the ceca by colonic antiperistalsis (Duke 1986a). This villous meshwork exists even in species, such as the House Sparrow (*Passer domesticus*), with very small, possibly nonfunctional, ceca (Klem et al. 1983). In the few species with larger ceca that have been studied histologically in detail (domestic chickens, *Gallus,* other galliforms, and ducks, *Anas*; Calhoun 1954, Clarke 1978, Fenna and Boag 1974b, Mahdi and

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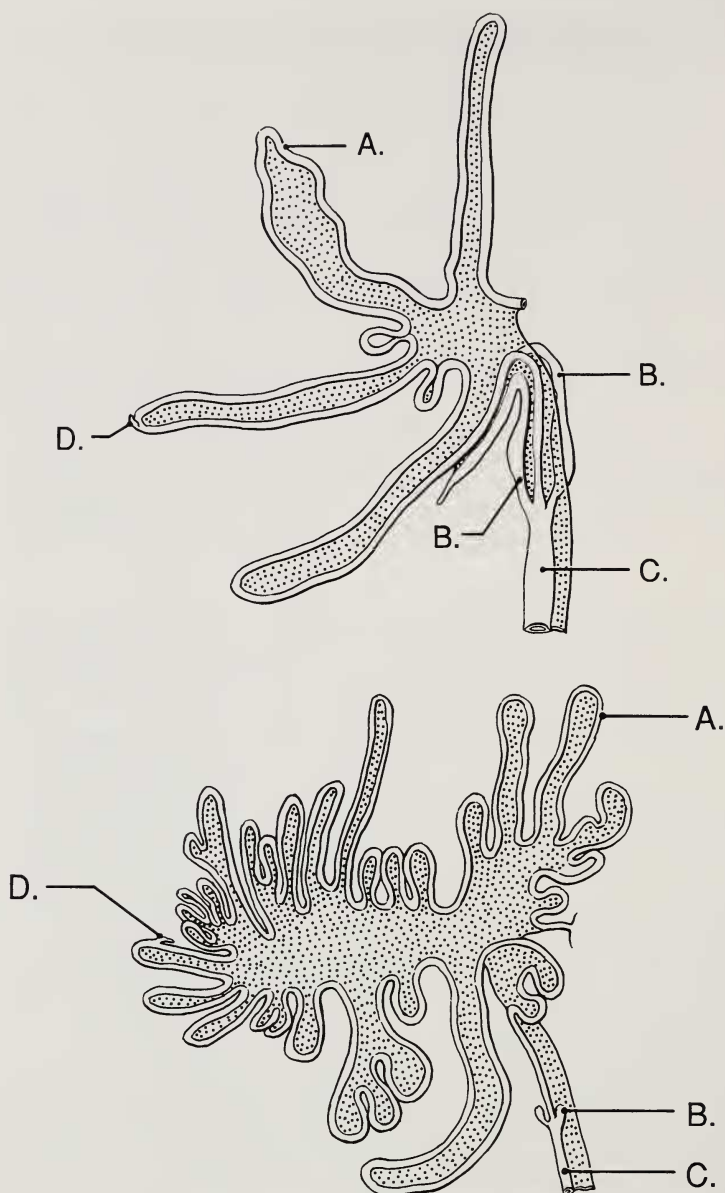
FIG. 1.   Diagrammatic representation of avian digestive tracts distal to the stomach. (Top) Little Grebe (*Tachybaptus ruficollis*) and (Bottom) Jackass Penguin (*Spheniscus demersus*). (A) small intestine; (B) ceca; (C) colon; (D) Meckel's (vitelline) diverticulum. Redrawn from Mitchell (1901).

TABLE 1
CECAL CHARACTERISTICS BY ORDINAL GROUPS

| | Size (paired) | | | |
	Large	Moderate	Small/ vestigial	Absent	Remarks
Struthioniformes	X				
Rheiformes	X				
Casuariiformes		X			
Apterygiformes	X				
Tinamiformes	X				
Sphenisciformes			X		
Gaviiformes		X			
Podicipediformes		X	X		
Procellariiformes			X		Single in some spp. Variable, see text
Pelecaniformes			X		Single in some spp.
Ciconiiformes			X		Single in some spp.
		X			Phoenicopteridae
Anseriformes	X	X			*Mergus*: reduced
	X				*Chauna, Anhima*
Falconiformes			X		Some *Falco*: single
Galliformes	X				
Gruiformes	X				*Eurypyga*: small
Charadriiformes	X	X	X		Variable, see text
Columbiformes			X	X	Pteroclididae: large
Psittaciformes				X	
Cuculiformes	X	X		X	Variable, see text
	X				*Opisthocomus*
Strigiformes	X				
Caprimulgiformes	X				*Aegotheles*: absent
Apodiformes				X	
Coliiformes				X	
Trogoniformes		X			
Coraciiformes		X	X	X	Variable, see text
Piciformes				X	Galbulidae: small
Passeriformes			X		

McLelland 1988), the ceca have been found to have a well-developed basal ring of circular muscle forming a sphincter (not a flap valve, as some of the early literature suggested). The terminal ileum protrudes slightly into the proximal colon as an ileal papilla and also has a sphincter. From their bases, ceca usually extend orad on either side of the ileum and are loosely attached to it by mesentery and the ileocecal ligament. Certain birds, notably herons, have a single cecum. The Secretary-bird (*Sagittarius serpentarius*) has been reported, probably erroneously, to

have two pairs (Maumus 1902). Although the gross structure of most ceca is that of a simple blind-ended tube, others are morphologically complex; a few have internal folds or spirals, and in at least one species (Elegant Crested Tinamou, [*Eudromia elegans*]), the ceca contain multiple sacculations, resulting in structures that look much like two bunches of fused grapes.

As with many aspects of avian morphology, most ceca were described in the late 19th and early 20th centuries, the descriptions often being incidental to other studies. Of particular importance are the works by Beddard (1898), Mitchell (1901), and Maumus (1902). A later contribution to the field was made by Naik (1962), but only abstracts from that work (a thesis for an M.Sc. degree, Banaras Hindu Univ.) have been available in the published literature. Fortunately, a carbon copy of the thesis was sent to John McLelland who wrote a review of cecal gross anatomy (1989) and who has generously lent the thesis to us. Photocopies of Naik's important study of Indian birds, including histological descriptions and figures of the gross morphology of 80 species (33 families in 15 orders), have now been deposited in the Division of Birds Library, The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, and the Wilson Ornithological Society's Van Tyne Memorial Library at the Univ. of Michigan, Ann Arbor. Some of Naik's figures are included here (Fig. 2).

CECAL TYPES AND OCCURRENCE

Naik (1962) classified avian ceca into five histological types: (1) Intestinal—long ceca that are histologically similar to the small intestine, (2) Glandular—long and well-developed ceca with an abundance of glandular (especially goblet) cells and capable of profuse secretory activity, (3) Lymphoid—small ceca with many lymphocytes, (4) Vestigial—very small ceca, often embedded in the intestinal wall, with little or no lumen, and (5) Absent.

The following survey of the occurrence of cecal types by avian orders has been compiled from the relatively sparse available records. Unless otherwise noted, the information has been abstracted from Mitchell (1896a, 1901), Beddard (1898, 1911), Maumus (1902), Naik (1962), and McLelland (1989). We have also examined a few genera in alcohol-preserved specimens in the collections of The Carnegie Museum of Natural History (CM) and the National Museum of Natural History, Smithsonian Institution (USNM). Although we have not listed all the species for which ceca have been described, the genera whose ceca have been figured are specified at the end of each ordinal account. Cecal types are as given by Naik (1962); those he did not examine are noted with a (?). Cecal sizes
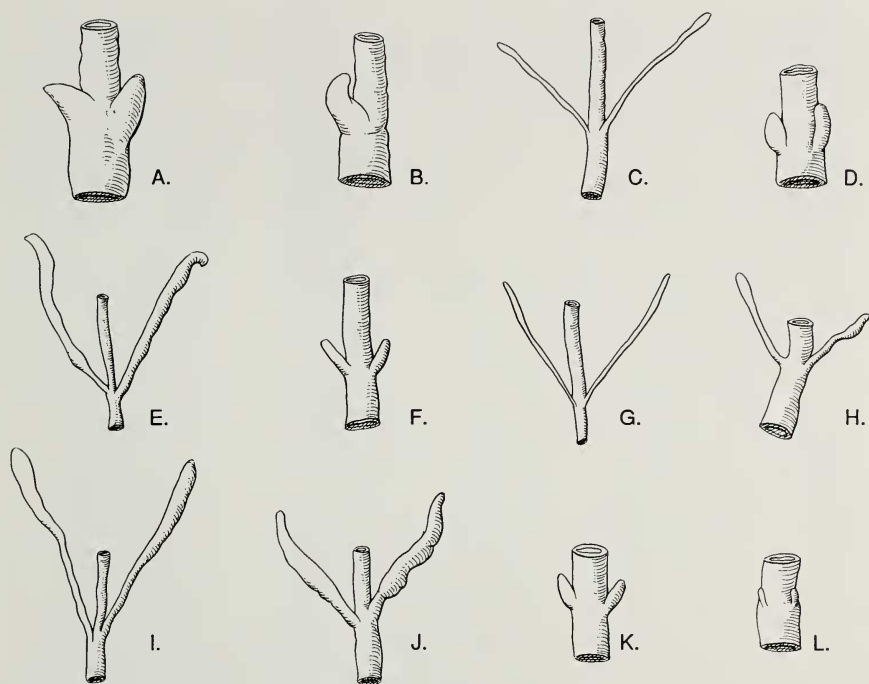
Fig. 2. Avian ceca: (A) Little Cormorant (*Phalacrocorax niger*), (Pelecaniformes) ×2.4; (B) Cattle Egret (*Bubulcus ibis*), (Ciconiiformes) ×2.4; (C) Cotton Teal (*Nettapus coromandelianus*), (Anseriformes) ×1.2; (D) Crested Serpent Eagle (*Spilornis cheela*), (Falconiformes) ×2.4; (E) Common Quail (*Coturnix coturnix*), (Galliformes) ×1.2; (F) Collared Dove (*Streptopelia decaocto*), (Columbiformes) ×3.2; (G) Redwattled Lapwing (*Vanellus indicus*), (Charadriiformes) ×0.8; (H) Common Koel (*Eudynamys scolopacea*), (Cuculiformes) ×2.0; (I) Spotted Owlet (*Athene brama*), (Strigiformes) ×1.2; (J) Indian Roller (*Coracias benghalensis*), (Coraciiformes) ×1.6; (K) Oriental Skylark (*Alauda gulgula*), (Passeriformes) ×4.0; (L) Gray Wagtail (*Motacilla cinerea*), (Passeriformes) ×3.2. Redrawn from Naik (1962), relative sizes indicated.

("large," "small") are relative to body sizes. With a few exceptions (e.g., *Opisthocomus*), the taxonomy followed is that of Morony et al. (1975).

Struthioniformes.—Intestinal type (?) Large and very long ceca (56–95 cm), externally fingerlike with a tapering tip and a well-developed internal valve-like helical fold that is reflected in the spiral shaping of the organ's exterior. The cecal wall is thin at the base, but thickens toward the apex. Although ostrich ceca are paired, they have a common orifice into the dorsal colon. This single cecal opening is present in all ratites. The ostrich colon is also very long (1640 cm), partly sacculated, and looped, unlike that of almost all other birds. Mitchell 1896a, Maumus 1902, Bezuidenhout 1986, *Struthio.*

Rheiformes.—Intestinal type (?) Even longer (42–142 cm), the ceca of rheas have less internal spiral folding than in ostriches; the colon is also long. Mitchell 1901, Maumus 1902, *Rhea.*

Casuariiformes.—Intestinal type (?) For large-bodied ratites, cassowaries have ceca that are relatively short (8–18 cm), but with sacculations; the colon is also short (29 cm; Herd and Dawson 1984, Herd 1985). Mitchell 1896a, *Casuarius.*

Apterygiformes.—Intestinal type (?) The ceca of kiwis are comparatively large (18 cm) and relatively wide, with less sacculation than in ostriches or rheas. Mitchell 1901, Maumus 1902, *Apteryx.*

Tinamiformes.—Intestinal type (?) Tinamou ceca are long (6–24 cm) and externally simple and fingerlike in *Tinamus, Crypturellus* (Fig. 3), and *Nothura.* We have externally examined, but not dissected, Brushland Tinamou (*Nothoprocta cinerascens*) (CM A-2369) and Small-billed Tinamou (*Crypturellus parvirostris*) (CM A-5330) and also found them simple. In contrast, the ceca of *Rhynchotus* are long, with an internal spiral structure; this is reflected in their external morphology.

The paired ceca of the Elegant Crested Tinamou are extraordinary and probably unique within Aves (Fig. 3): long and wide (12.5–13.0 × 2.2–2.5 cm; Wetmore 1926) and internally honeycombed by many small diverticula. These outpocketings gradually diminish in size and organization from the base to the tip of the organ, apically showing a more spiral form of internal ridges like ratite ceca. Externally, the basal diverticula protrude from the ceca as pointed lobes, gradually becoming flatter but still clearly apparent toward the organ's tip. Beddard 1890a, *Eudromia*; Beddard 1898, *Nothura*; Mitchell 1901, Maumus 1902, *Rhynchotus.*

Sphenisciformes.—Vestigial type (?) Penguin ceca are very small to vestigial (2–4 cm), whereas the small intestine is very long (178 ± 16 cm in chicks of the Gentoo Penguin, *Pygoscelis papua*; Roby et al, 1989). Mitchell 1896a, *Eudyptes*; Mitchell 1901, *Spheniscus* (Fig. 1), *Aptenodytes.*

Gaviiformes.—Intestinal type (?) Loons have moderately short (4–5 cm) and slender ceca with irregular internal sacculations. Mitchell 1896a, 1901, *Gavia.*

Podicipediformes.—Intestinal type (?) Grebe ceca are small (3–4 cm in *Podiceps,* but longer in *Tachybaptus*) and structurally apparently like those of loons. Mitchell 1901, *Podiceps*; Mitchell 1901, Beddard 1911, *Tachybaptus* (Fig. 1).

Procellariiformes.—Vestigial type (?) Ceca are generally small, nipplelike, or lacking (0–1 cm) in the tubenoses. Some species may have only one cecum, but in such cases one or both could have been overlooked, being obscured by fat or mesenteries or embedded in the intestinal
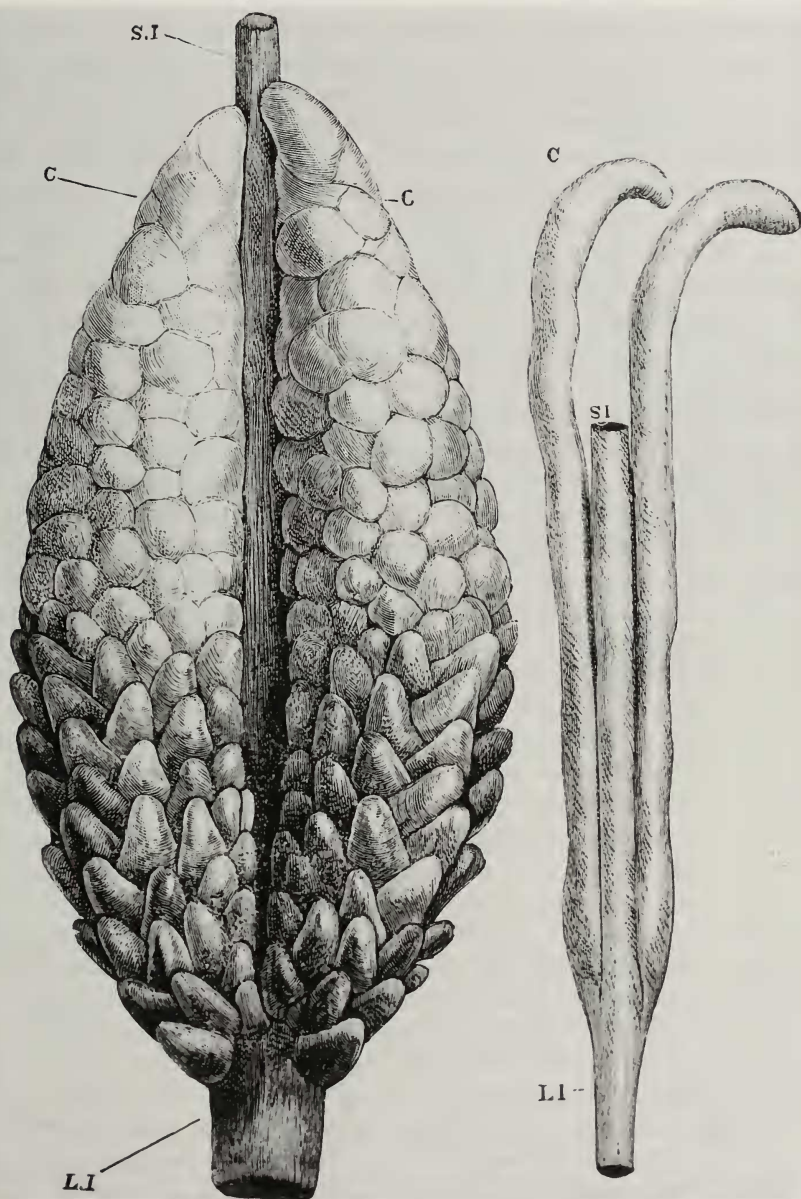
FIG. 3. Ceca of Elegant Crested Tinamou (*Eudromia elegans*) (left) and Spotted Tinamou (*Nothura maculosa*) (right). From Beddard (1898).

wall. However, G. Duke (pers. comm.) reports that Leach's Storm-petrel (*Oceanodroma leucorhoa*) has a single, relatively large cecum that is nearly as long as its colon. Mitchell 1896a, *Fulmarus*; Mitchell 1901, *Diomedea*; Kuroda 1986, *Pterodroma, Puffinus.*

Pelecaniformes.—Lymphoid type. The ceca of totipalmate swimmers are small (0.5–5 cm) in Pelecanidae and Phalacrocoracidae, and vestigial (<0.5 cm) in Phaethontidae, Sulidae, and Fregatidae. Only one cecum is visible in some specimens, although a second may be present. Mitchell 1901, *Phaethon, Sula, Phalacrocorax, Anhinga* (single cerum), *Fregata, Pelecanus*; Maumus 1902, *Pelecanus*; Naik 1962, *Phalacrocorax* (Fig. 2).

Ciconiiformes.—Lymphoid type. The ceca of herons and their allies are variable: reduced, small, or rudimentary in all but flamingos. Species with paired ceca often have one smaller than the other. Ciconiidae have two small ceca (0.3–1.5 cm); Scopidae also have two, as do Threskiornithidae (0.3–1.0 cm). Ardeidae usually have a single small cecum (0.4–1.0 cm), although careful examination may reveal a second rudimentary one in the wall of the intestine. Balaenicipitidae also have a single cecum. Phoenicopteridae, in contrast, have a relatively well-developed (8 cm) fingerlike pair, probably of the intestinal type. Mitchell 1896a, *Ciconia, Platalea*; Mitchell 1901, *Ardea, Nycticorax, Phoenicopterus, Mycteria, Scopus*; Maumus 1902, *Leptoptilos, Cochlearius, Mycteria, Ardea*; Naik 1962, *Anastomus, Bubulcus* (Fig. 2), *Nycticorax, Egretta, Ardeola.*

Anseriformes.—Intestinal type. The ceca of ducks and geese are generally moderate to long (4–38 cm), with exceptions such as reduced paired (0–5 cm), single, or absent ceca in *Mergus* and *Melanitta* (Goudie and Ryan 1991). Barnes and Thomas (1987) found a correlation between anatid cecal size (mass) and diet: herbivores have larger ceca than carnivores, and omnivores are intermediate. The screamers (*Chauna*, Anhimidae) are a major exception in that the ceca are large (8 cm), almost bulbous in appearance, sacculated internally, and followed by a large looped colon. *Anhima* has similar, but smaller, ceca. Mitchell 1896a, *Cygnus, Chauna*; Beddard 1898, *Chauna*; Mitchell 1901, *Mergus, Anseranas, Anas, Nettapus, Anhima*; Maumus 1902, *Mergus, Anas, Chauna*; Naik 1962, *Anas, Nettapus* (Fig. 2); Mattocks 1971, *Anser*; McLelland 1991, *Anas.*

Falconiformes.—Lymphoid type. The ceca of eagles, hawks, vultures, and other birds of prey are very small, vestigial, or absent (0–2 cm). Mitchell 1896a, *Haliaeetus*; Mitchell 1901, *Cathartes* (ceca absent), *Neophron, Gypohierax, Polyborus, Circus, Falco, Pandion*; Maumus 1902, *Accipiter*; Beddard 1911, *Polemaetus, Cathartes*; Naik 1962, *Milvus, Neophron, Gyps, Spilornis* (Fig. 2).

Mitchell's figure (1901) of the Secretary-bird, does not include the lower colon where Maumus (1902) recorded finding a second pair of ceca.

Beddard (1898) examined four specimens of *Sagittarius* and noted nothing unusual about their ceca (0.4–0.6 cm long), nor did he mention a second, distal pair. Maloiy et al. (1987) reported that two specimens they examined had a single pair of very small "cecal buds;" one specimen is figured. In light of these studies, the otherwise unremarkable intestinal tract of the Secretary-bird as discussed in detail by Mitchell (1901), and the generally poor cecal development of the Falconiformes, we are inclined to believe that Maumus mistook an anomaly or perhaps a pathological condition for a (figured) budlike "second pair" of ceca 9 cm from the cloaca; a "normal" pair, figured as having a long thin stalk with a greatly expanded tip, was 125 cm proximal to the cloaca and in the usual location for ceca.

Galliformes.—Intestinal type. The best developed of the intestinal type, gallinaceous ceca range from long to very long (6–34 cm), with extreme lengths of 35–92 cm in certain grouse in winter (Moss 1983). The ceca usually widen apically or end in a bluntly rounded tip rather than tapering at the apex and may contain internal submucosal folds. The Satyr Tragopan (*Tragopan satyra*) is the only galliform known to have sacculated ceca (McLelland 1989). Beddard (1911) described the Crested Bobwhite (*Colinus cristatus*) ("*Eupsychortyx sonnini*") as having ceca that were spirally coiled and covered by a loosely meshed network of bands containing a great deal of fat. We suspect this quail had seasonally enlarged ceca, as is now known to occur in many other galliforms. Mitchell 1896a, *Argusianus*; Mitchell 1901, *Alectura, Crax, Pavo*; Maumus 1902, *Numida*; Beddard 1911, *Alectura*; Leopold 1953, *Callipepla*; Naik 1962, *Coturnix* (Fig. 2), *Gallus*. Peckham (1965) reported a cecal anomaly in *Gallus*: a chicken with a single cecum that was bifurcated at the tip.

Gruiformes.—Intestinal type. The diverse order of cranes, rails, and allies has generally large ceca (2.5–37.0 cm), with the exception of the Sunbittern, *Eurypyga helias* (0.6 cm). In the Otidae (*Otis* [27 cm], *Coriotis* [24 cm], and *Eupodotis*), the long cecum is unusual: the basal third has internal villi; the middle third is dilated, lined with a smooth mucous membrane, slightly partitioned by longitudinal folds (but no sacculations) and scattered with many glands; and the apical third has a netlike mucous membrane. Most of the gruiform families have been described. Mitchell 1896a, *Crex, Cariama*; Mitchell 1901, *Turnix, Tricholimnas, Grus, Aramus* (only 5–8 cm long, but wide), *Psophia, Otis, Rhynochetos, Heliornis*; Maumus 1902, *Otis, Porphyrio, Aramides*; Beddard 1911, *Eupodotis*; Naik 1962, *Amaurornis, Turnix*; Sitna 1965, *Fulica*; Maloiy et al. 1987, *Choriotis*.

Charadriiformes.—Intestinal type. Shorebird ceca are variable: rudimentary in Jacanidae, some Scolopacidae (*Scolopax, Eurynorhynchus*),

Laridae (short in *Anous* but long in *Gygis*), Rhynchopidae, and Alcidae (but 3 cm in *Alca*); moderately large (2–9 cm) in Hematopodidae, Recurvirostridae, Burhinidae, Glareolidae, Charadriidae, most Scolopacidae, Thinocoridae, and Stercorariidae; and very large (21–23 cm) in sheathbills, Chionidae. The long ceca are fingerlike in shape and frequently tapered at the tip. Mitchell 1896a, *Numenius, Scolopax, Larus*; Mitchell 1901, *Calidris, Chionis, Glareola, Thinocorus, Jacana, Pagophila, Stercorarius, Sterna, Fratercula, Uria*; Maumus 1902, *Alca, Numenius*; Beddard 1911, *Pluvianus, Fratercula*; Naik 1962, *Vanellus* (Fig. 2).

Columbiformes.—Lymphoid or vestigial types. Ceca are very small or (mostly) entirely absent in pigeons (Columbidae) but large (intestinal type?) with internal folds and a common orifice into the colon in sandgrouse (Pteroclididae; 12 cm in *Syrrhaptes*). Mitchell 1896a, *Pterocles, Columba*; Maumus 1902, *Pterocles*; Naik 1962, *Columba, Streptopelia* (Fig. 2); McLelland 1991, *Columba*.

Psittaciformes.—Ceca are entirely absent in parrots, without a trace in embryos or adults. Mitchell 1896a, *Ara*; Mitchell 1901, *Strigops*; Beddard 1911, *Nestor*.

Cuculiformes.—Intestinal type. The ceca of cuckoos (Cuculidae) are moderate to long (2–6 cm in most, 17 cm in *Scythrops*) but absent in touracos (Musophagidae). The tip is expanded in roadrunners, *Geococcyx*.

The large ceca of *Opisthocomus* are like those of gallinaceous birds but also like those of cuckoos. Other parts of the Hoatzin's digestive tract show extreme specializations—a large crop that has been demonstrated to digest vegetation (Grajal et al. 1989) and a long colon with convolutions (of unknown function) similar to those of ratites and *Chauna*. Mitchell 1896a, *Tauraco*; Mitchell 1896b, *Opisthocomus*; Mitchell 1901, *Carpococcyx*; Maumus 1902, *Opisthocomus*; Marshall 1906, *Geococcyx*; Naik 1962, *Eudynamys* (Fig. 2), *Clamator, Centropus*; Grajal et al. 1989, *Opisthocomus*.

Strigiformes.—Glandular type. The ceca of most owls are generally large (4–11 cm) and distinctively shaped: the apical half is expanded to a greater or lesser degree. An extreme example of this differentiation is found in *Phodilus* (Beddard 1890b), where each cecum is a bulbous organ at the end of a thin, stalk-like tube that connects it to the colon. We have briefly examined a preserved *Tyto alba* (CM A-24479): each cecum looks like a swollen leaf with a narrow stalk-like base and a greatly expanded, clearly glandular apex that has the superficial appearance of bleached liver. Judging from the conflicting descriptions of owl ceca in the literature, the degree of apical dilation may be individually variable, with some specimens showing little or no expansion. The recorded variation in owls may be seasonal (like expanded grouse ceca in winter) or it may be a

response to other dietary or environmental changes. Mitchell 1896a, Marshall 1906, *Bubo*; Mitchell 1901, Maumus 1902, *Strix, Asio*; Beddard 1911, *Asio*; Naik 1962, *Tyto, Bubo, Athene* (Fig. 2), *Glaucidium.*

Caprimulgiformes.—Glandular type (?) Nightjars (Caprimulgidae) and frogmouths (Podargidae) have large (3–5 cm) ceca, the apical half dilated like those of some owls. Oilbirds (*Steatornis*) are also reported to have long paired ceca (Bosque and de Parra 1992). Owlet-frogmouths (Aegothelidae) lack ceca. Mitchell 1901, *Nyctidromus*; Marshall 1905, *Phalaenoptilus.*

Apodiformes.—Ceca are absent in both swifts and hummingbirds. Mitchell 1901, *Apus*; Marshall 1906, *Aeronautes.*

Coliiformes.—Colies also lack ceca. Mitchell 1896a, *Colius.*

Trogoniformes.—Intestinal type (?) Trogon ceca are moderate in length (3–5 cm). Mitchell 1901, *Trogon.*

Coraciiformes.—Intestinal, glandular (*Coracias*), or absent types. Most of the kingfishers and allies lack ceca: Alcedinidae, Momotidae, Upupidae, Phoeniculidae, and Bucerotidae. In the other families (so far as is known), the ceca are apically dilated like those of owls. They are short (1–3 cm) but wide in bee-eaters and todies (Meropidae and Todidae); in the Puerto Rican Tody (*Todus mexicanus*) (CM A-832) the ceca are 7 mm long and about 1 mm wide, slightly broader at the apex. Rollers and cuckoo-rollers (Coraciidae and Leptosomatidae) have long ceca (4–7 cm). Mitchell 1896a, *Aceros*; Mitchell 1901, *Coracias, Dacelo, Merops, Upupa*; Naik 1962, *Merops, Coracias* (Fig. 2).

Piciformes.—With the exception of jacamars (Galbulidae), which have short (2 cm) ceca, the organ is absent in all families of woodpeckers and allies, including honeyguides and puffbirds (Indicatoridae and Bucconidae: Lesser Honeyguide [*Indicator minor*], USNM 290581; Spotted Puffbird [*Bucco tamiata*], CM A-1308). Beddard (1898:186) noted that ceca are "exceptionally present" in the Eurasian Green Woodpecker (*Picus viridis*) and he later (1911) figured a specimen lacking ceca, but it is generally true that in species that normally lack ceca, individuals are occasionally found with vestigial organs. Mitchell 1901, *Megalaima*; Beddard 1911, *Melanerpes.*

Passeriformes.—Lymphoid or vestigial types. Passerine ceca are small or rudimentary and nipple-like (<0.1–1.5 cm) but apparently never completely absent. The ceca have thick walls and a very small lumen. In the largest passerine, the Superb Lyrebird (*Menura novaehollandiae*) (CM A-1834), the ceca are 1.2 cm long and 0.3 cm wide. Mitchell 1896a, *Parus*; Mitchell 1901, *Corvus*; Maumus 1902, *Poephila*; Beddard 1911, *Gymnorhina*; Klem et al. 1983, *Passer*; Klem et al. 1984, *Turdus*; McLelland 1991, *Serinus.* Naik (1962) figured 35 species (26 genera) in 14 passerine

families (taxonomy as used by Naik): Alaudidae (1; *Alauda,* Fig. 2), Lan-
iidae (1), Oriolidae (1), Dicruridae (1), Sturnidae (6), Corvidae (3), Cam-
pephagidae (2), Pycnonotidae (2), Muscicapidae (5), Motacillidae (4; *Mo-
tacilla,* Fig. 2), Nectariniidae (2), Ploceidae (5), Fringillidae (1), and
Emberizidae (1); all specimens had small paired ceca, ranging from 0.05
to 1.15 cm in length.

This ordinal summary demonstrates that correlation between cecal size
and systematic position is weak except among closely related species.
However, since the early studies (e.g., Mitchell 1901), workers have noted
a general relationship between cecal development and diet. In broad
terms, herbivores have larger ceca and carnivores have smaller ones. Naik
(1962) observed that ceca tend to be well-developed in Indian herbivores,
omnivores, and birds that feed on molluscs (but see Goudie and Ryan
1991); they are variable in insectivores and carnivores and small in pis-
civores and graminivores (McLelland 1989). However, on a world-wide
basis, the exceptions are many. For instance, hawks and owls with basi-
cally similar carnivorous diets have ceca of very different sizes and his-
tologies. Fish-eating species fall into several different cecal size catego-
ries: loons and grebes have relatively well-developed ceca, penguins have
small-to-vestigial ones, and kingfishers have none at all. Insectivores
range from large-to-moderate ceca in nightjars, trogons, and bee-eaters,
through small-to-vestigial in insectivorous passerines, and are absent in
swifts and hummingbirds. It is probable that dietary changes resulting
from such variables as seasonal availability of food types, individual pref-
erences, and age effects strongly modify genetic influences on cecal struc-
ture. Non-dietary factors also may be more important than food in some
species.

CECAL FUNCTIONS

Cecal functioning is still only partly understood (McNab 1973, Braun
and Duke 1989). Although early investigations searched for a single func-
tion of the organ, it is now clear that the cecum has the potential to act
in many different ways. And depending on the species involved, the cecal
morphology, and the ecological conditions under which a bird lives, those
functions can be vitally important to its physiology—perhaps especially
so during periods of stress. It is also apparent that the avian cecum *can*
function in a highly efficient manner, even more efficiently than the cecum
of most mammalian herbivores in terms of size and fermentation rates
(Gasaway 1976b).

The intestinal type of cecum in birds is a blind-ended sac with a mesh-
work of long interdigitating villi at its entrance. The majority of cecal
villi apparently act as a sieve, allowing fluid and fine particles to enter

the cecal lumen as colonic contents are pushed against and selectively past the cecal sphincter by retrograde waves of colonic muscle contraction (Fenna and Boag 1974a). At the same time, this material is prevented from moving up into the ileum by the contracted ileal sphincter. The colonic motility probably also rinses water-soluble substances and fine particles from the colonic contents and pushes them into the ceca (Björn-hag 1989). Because a cecum is blind-ended, its contents can be retained for longer periods than would be possible in the main (small or large) intestine through which digesta move relatively rapidly (e.g., Shibata and Sogou 1982, Clench and Mathias 1992). Held in the ceca, fluid has time to be absorbed and molecules in solution as well as solid particles can be acted on by bacteria, fungi, and other micro-organisms (Duke 1986b). It is also now appreciated that the mixing action produced by cecal wall contractions keeps the contents in general motion; cecal motility also contributes to filling and evacuating the organ (Duke 1986a, Clench and Mathias, unpubl. data). Thus, at different times and under different conditions, the cecum has been found to be a site for fermentation and further digestion of food (especially for breakdown of cellulose), for utilization and absorption of water and nitrogenous components, for microbial action of both beneficial and disease-causing organisms, and as a site for production of immunoglobulins and antibodies.

Study subjects.—Much of what is known about cecal physiology is based on studies of gallinaceous birds and waterfowl: the intestinal type of cecum. These birds (and their ceca) are large enough to study easily. Domestic and semidomestic species (chickens, quail, pheasants; domestic ducks and geese) also are readily available, they are behaviorally more amenable to manipulation, and their economic importance leads to research funding. Unfortunately, however, most domestic birds (notably chickens) have proved to be exceptionally poor models for the study of cecal function. This is probably because, through the genetic changes resulting from domestication, and the almost universal use of commercial, nutritionally complete, poultry feed (even "enhanced" with antibiotics), the average chicken cecum has lost much or all of its natural microflora and -fauna and its potential physiological capabilities (Thomas 1987). A chicken fed on whole natural grains that require more "digestion" produces results more like those from wild birds (unpubl. data). A cecectomized chicken seldom differs significantly from the intact bird in growth or other physiologic indicators (Thornburn and Willcox, 1965). Consequently, older literature abounds with contradictory and confusing reports based on studies of domestic fowl (McNab 1973). A clearer picture of natural cecal function is only now beginning to emerge.

Because some popular game species—grouse, ptarmigan, and allies

(Tetraoninae)—undergo spectacular annual cecal changes, the study of their digestive system is both economically important and theoretically interesting. However, domesticated individuals of wild species, or even birds recently captured from the wild, may produce data that are significantly different from data obtained from the natural condition. For example, Moss (1972) used Red Grouse (*Lagopus lagopus scoticus*) to show the striking effects of captivity on cecal length. The mean cecal (combined) length from 29 wild males was 144 cm, whereas measurements from birds raised from eggs taken from natural nests were significantly shorter. Cecal lengths continued to decrease each generation the grouse were away from the wild, and ceca were 54% shorter than those of wild birds by the fourth year, when the experiment ended. Many other studies (e.g., Moss and Parkinson 1972; Moss 1974, 1977; Hanssen 1979a) have also demonstrated major differences in gut length and digestive capability in the ceca of wild vs captive galliforms.

Ceca in captives and domestic birds usually have a poorer microfauna and -flora than those of wild individuals. Hanssen (1979a, b) showed that cecal microanatomy and -biology of wild vs captive Willow Grouse (*L. l. lagopus*) were very different. Additionally, unless ceca are allowed sufficient time to adjust to changes in diet or other variables being studied, results may not be physiologically accurate. Subjects are often allowed only a few days to a week to adapt to a new diet (e.g., Inman 1973), when it may take considerably longer than that—4 to 12 weeks—for acclimatization (Savory and Gentle 1976, Moss 1977, Kenward and Sibly 1978, Duke et al. 1984, Moss 1989, Redig 1989). The common use of domestic birds with a limited cecal microbiota has also seriously handicapped attempts to apply principles obtained from those studies to cecal functioning in wild species. Moss (1989:61) suggested that galliform digestion may function in two modes: "1) a low-fiber mode, in which bulk does not limit intake and fiber digestion is unimportant, and 2) a high-fiber mode, in which bulk limits intake and fiber digestion may well be important." He also noted (loc. cit.) that "most studies on avian digestion have been of captive galliforms, most of which probably function in low-fiber mode all the time. Wild galliforms seem to function in high-fiber mode for much of the time. . . ." The low-fiber mode includes shorter, unmodified ceca that are probably unnecessary for digestion of artificial diets. However, Moss also showed that certain intestinal tract data from captives fell onto the same regression lines as those from free-living wild birds, indicating that some information could be usefully extrapolated from one to the other.

Diet and changes in cecal length.—Considerable research, particularly with anseriform and galliform species, has been conducted on how diet

affects cecal size. Captives have often been used to demonstrate different dietary effects on cecal length and mass (e.g., Mallards [*Anas platyrhynchos*]; Miller 1975, Kehoe et al. 1988). Wild birds have also been used in the same sorts of studies. For example, Sitna (1965) compared small samples of captive vs wild Eurasian Coots (*Fulica atra*). Her birds were kept for >16 months on diets of plants, starch, or fish, and all had shorter ceca (15.6 to 18.8 cm) than those of coots collected from the wild (24.2 cm).

Particular attention has been paid to the increase in grouse cecal lengths and masses in winter, when the birds are feeding on a poorer, more fibrous diet. Although cecal lengths and masses do not measure the same thing, they do indicate a general size increase. It is unknown, for instance, whether heavier ceca result from muscle hypertrophy or cell proliferation (of any type), or if cecal lengthening is produced by cell proliferation or is a simple distention of an elastic organ in response to more bulk in the lumen.

Mortensen et al. (1985) showed that in Norwegian Rock Ptarmigan (*Lagopus mutus*) ceca more than doubled in mass, from 22 g in September to a peak of 48 g in March. Thomas (1984) found that in Willow Ptarmigan (*L. lagopus*) in Ontario, winter cecal masses of males were 10.2 ± 3.0 g, but then decreased to 5.5 ± 0.6 g in spring; females were similar, going from 9.1 ± 1.9 g to 5.7 ± 0.6 g. The ceca also were much longer in winter, with a combined length of 119.4 ± 10.8 cm in males and 114.0 ± 7.6 cm in females. The same species in Finnish Lapland may have even longer winter ceca—140.0 ± 10.0 cm in males, 129.7 ± 7.2 cm in females (Pulliainen and Tunkkari 1983). Pulliainen (1976) also showed in a sample of 282 birds that *L. lagopus* in Lapland have winter ceca longer than the small intestine—124.5 ± 1.1 cm and 93.8 ± 0.6 cm, respectively. Even the ceca of California Quail (*Lophortyx californicus brunnescens*) living in a moderate climate, but where the winter diet is exclusively low-quality bulky greens, lengthen from 8 cm in summer to 12.5 cm in winter; the villi also increase in length at the same time (Lewin 1963). Pendergast and Boag (1973) showed that the ceca of wild male Alberta Spruce Grouse (*Canachites canadensis*) were also significantly longer and heavier ($P < 0.01$) in winter—410 mm in February vs 340 mm in April. However, captives from the same population that were maintained mostly on poultry feed did not have the same size or degree of seasonal change—270 mm vs 170 mm, winter vs summer. Moss (1989) has shown that cecal lengthening in response to an increase in dietary fiber is not linear; significant lengthening occurs only after a critical percentage of fiber in the diet has been reached.

In wild North American Anatidae, Barnes and Thomas (1987) found

that a guild of six carnivorous duck species had significantly smaller ceca ($P < 0.0001$) than three omnivorous species with intermediate-sized organs that, in turn, differed significantly ($P < 0.0001$) from nine herbivores with large ceca. Gizzard and small-intestine masses reflected the same differences. Kehoe and Ankney (1985) reported that in five species of diving ducks (*Aythya*), cecal length was greatest in *A. americana,* intermediate in *A. affinis, A. collaris,* and *A. marila,* and least in *A. valisineria,* which directly correlated with the amount of fiber in their respective diets. Goudie and Ryan (1991) noted that Black Scoters (*Melanitta nigra*), feeding almost exclusively on mussels (*Mytilus edulis*), had very short ceca (ca 2 cm) compared with four other sea duck species with more diverse diets. Paulus (1982) reported that both sexes of Gadwalls (*Anas strepera*) had heavier ceca in January and February, when they were feeding on higher-fiber foods, than they had in November. Halse (1984, 1985) found seasonal changes in Egyptian Geese (*Alopochen aegyptiacus*) and Spur-winged Geese (*Plectropterus gambensis*): the ceca hypertrophied significantly ($P < 0.05$) during the wing molt when the birds were flightless and their main diet changed from corn to water plants. Drobney (1984) reported that cecal lengths of female Wood Ducks (*Aix sponsa*) increased between the fall courtship and egg-laying periods ($P < 0.001$), whereas those of males decreased during the same period ($P < 0.001$). In contrast, Ankney and Afton (1988) found no difference in prelaying vs laying-period cecal lengths and masses in male and female Northern Shovelers (*Anas clypeata*); they noted also that shovelers are relatively more carnivorous than other waterfowl. In all these studies of anseriforms, it was concluded that the gut changes resulted from a complex of factors, especially (but not always) an increase in dietary fiber and differences in quantity of food consumed.

Digestion and fermentation.—A convincing demonstration of cellulose digestion, fermentation, and absorption of nutrients from avian ceca has taken many years (McNab 1973). This delay may have resulted largely from the study of domestic fowl lacking dietary preconditioning and appropriate bacteria (Gasaway 1976b, Duke et al. 1984). The process of collecting and culturing anaerobic microorganisms, even from wild birds with abundant cecal faunas, is also difficult (McBee and West 1969, Jayne-Williams and Fuller 1971). Only by study of wild birds, especially grouse, have some of the basic questions on cecal digestion begun to be answered.

The first proof that cecal bacteria could decompose cellulose was reported from the Eurasian Capercaillie (*Tetrao urogallus*) and Willow Grouse (*L. lagopus*) by Suomalainen and Arhimo in 1945. Shortly thereafter, Leopold (1953) suggested a relationship between intestinal length

and diet: the ceca of grouse that fed on low-quality, high-fiber browse averaged 136% longer than those of seed-eating galliforms. At the time, Leopold apparently did not realize that galliform ceca can lengthen in winter. By the late 1960s, cellulose digestion and fermentation in wild birds had become an active field of study, but some investigations were still marred by insufficient preconditioning before birds were fed new diets.

One of the first studies to demonstrate effective cecal fermentation used Alaskan Willow Ptarmigan (*L. lagopus*) (McBee and West 1969). In winter, this species feeds almost entirely on willow (*Salix*) twig tips and buds. In processing the food, gizzard action grinds the buds but it strips and grinds only the bark and cambium layers from the twigs. After passing down the small intestine, almost all the relatively nutritious and finely ground bud-bark-cambium paste is diverted into the ceca; the well-cleaned but undigested woody cores are passed into the colon for evacuation. Measurable amounts of fermentation products—lactic, acetic, propionic, and butyric acids and ethanol—were found only in the ceca, which were also the only site for significant numbers of bacteria, an average of 1.4×10^{11}/g of cecal contents (wet weight). The bacteria were difficult to culture, but anaerobes appeared to dominate—38.8% gram-positive rods, 47.9% gram-negative spirals or rods, and 13.6% gram-positive and -negative cocci. The authors estimated that 6% to 30% of the basal energy requirement of Willow Grouse in winter was supplied by cecal fermentation.

The contribution of ceca to avian nutrition has continued to be studied not only in grouse but also in waterfowl and other groups: Mattocks 1971, Moss and Parkinson 1972, Inman 1973, Thompson and Boag 1975, Miller 1976, Gasaway 1976a–d, Moss and Hanssen 1980 (review), Moss 1983, Herd and Dawson 1984, Buchsbaum et al. 1986, Dawson et al. 1989. Details of these studies cannot be included here, but in general they have shown that in species with well-developed ceca, significant proportions of dietary cellulose are digested and absorbed. The variation in fiber digestibility depends mostly on how much of the fiber can be processed into fine particles that, with soluble components, enter the ceca. Once in the organ, virtually all the cecal fiber is digested (e.g., an average of 96.8% in Blue Grouse, *Dendragapus obscurus*; Remington 1989).

Although almost all birds that include fermentation in their digestive processes do so in the ceca, a few have been shown to ferment food in other parts of the gut. Emus (*Dromaius*) have relatively short ceca but can ferment significant amounts of plant fiber in the distal small intestine and, to a lesser extent, the colon (Herd and Dawson 1984, Herd 1985). The South American Hoatzin (*Opisthocomus hoazin*), a rare avian foli-

vore, is the only bird known to ferment in the foregut; it has a specialized crop and esophagus in which the leaves that it feeds on are ground up and retained for long periods of time (~2 days) while cell walls are digested. The Hoatzin also, however, employs its large ceca for additional microbial fermentation (Grajal et al. 1989). New Zealand's Kakapo, *Strigops habroptilus,* is another avian obligate folivore, and like the Hoatzin, it has a specialized foregut. But unlike the Hoatzin, the nocturnal parrot probably cannot digest cellulose, relying instead on the extraction of cell contents from large quantities of vegetation (Morton 1978). As with all parrots, the Kakapo lacks ceca. Birds that primarily feed on vegetation either employ cecal fermentation or their digestive systems simply strip the easily obtained nutrients from plant material and quickly discard the rest. The New Zealand Takahe (*Notornis mantelli*) lacks morphological gut specializations and processes astounding amounts of grass. Reid (1974) reported that an adult Takahe can daily void ~8 m of feces from a gut that is <1.5 m long! Carrying a heavy load of digesting plant material is a serious drawback for flight efficiency, so it is not surprising that probably <3% of bird species are regular herbivores, and those that depend on bulky food are mostly or entirely flightless (Dawson 1989). Hoatzins are very poor fliers (pers. obs., M.H.C.). When grouse have expanded ceca in winter they fly poorly and reluctantly, and Emus, Kakapos, and Takahes are entirely flightless.

Utilization and absorption of water and nitrogenous compounds.—As investigations into cecal contents have become more detailed, and especially as their chemical processes have been analyzed, more attention has been paid to cecal functions in relation to fluids (e.g., salt and water balance, urine breakdown). The level of knowledge has now progressed to the point that absorption of fluids rather than nutrition has been suggested as the primary function of ceca in some species.

A landmark paper by Browne (1922) showed that fluid moved from the cloaca through the colon and into the ceca. It is now known that normal antiperistaltic motility of the colon moves its luminal fluids, including urine from the cloaca, proximally toward, and usually into, the ceca (but not the small intestine). This colonic antiperistalsis has been shown in Emus, various herons, ducks, geese, hawks, galliforms, gulls, roadrunners, owls, and crows (*Corvus*) (Akester et al. 1967, Ohmart et al. 1970, Clemens et al. 1975, Duke et al. 1984, Björnhag 1989). Many other (unstudied) birds probably also have this capability, but not all, even desert-dwelling species, do: an Australian cockatoo, the Galah (*Eolophus roseicapillus*) which, like all parrots, lacks ceca (Skadhauge 1976); some desert galliforms (Thomas et al. 1984); and ostriches (Skadhauge et al. 1984).

How important ceca are in the water balance of birds has been studied and debated for decades. It is now clear that the importance can vary with the species being studied, its age *and sex,* the degree of cecal development, and environmental stresses. Early studies of cecectomized chicks suggested that removal of the organ had no influence on water balance. But a later study of eight-month-old roosters showed that when more than two thirds of the ceca were removed, the birds drank significantly more water (P < 0.05) and produced 30% more fecal material, leading Isshiki and Nakahiro (1975) to conclude that ceca were important in water absorption, even in this domesticated species. Thomas (1982) noted that in birds with large ceca, water absorption occurs in ceca > colon > coprodeum. In a wild Alaskan galliform, the Rock Ptarmigan (*Lagopus mutus*), Gasaway et al. (1976) found that ceca were the major site of water absorption in the hindgut: 86% of water passing into the ileocecalcolic region was diverted into the ceca where virtually all (96%) of it was absorbed; 88% of the remaining 14% in the colon was passed out in feces. Gasaway et al. (1976) also noted, however, that the work of others had showed cecal water absorption to be less important in other wild galliforms (*Phasianus, Alectoris, Colinus*). Hughes et al. (1991) reported that the effects of cecal ligation differed in adult male and female domestic ducks when challenged by increased saline intake, but not when acclimated to fresh water.

When Duke et al. (1981) removed the glandular ceca of Great Horned Owls (*Bubo virginianus*), the birds drank more water during days 8–15 postoperatively, but then apparently compensated in some way for the cecal loss and returned to the same water intake levels as sham-operated birds had. This rapid compensation for cecectomy has also been shown in other species, leading to the conclusion that ceca were not vital to water balance, at least in most birds (Chaplin 1989). But when Chaplin measured the turnover of tritiated water in Great Horned Owls under low and high temperature conditions before surgical removal of the ceca and then again after allowing six weeks for recovery, she found water turnover was much higher. Excretory water loss was greatly increased (2.1× at 15°C and 4.8× at 27°C), but it could be offset by increased intake of food (rats) under 15°C and food and water under 27°C. Without supplementary food and water, the cecectomized birds could not maintain their body mass, and at 27°C also became dehydrated. Thus Chaplin (1989) concluded that ceca are vital to the water balance of those species that have them.

Assaying the microbiota contained in the cecal lumen has been another approach to studying cecal function (Barnes 1972, 1979). Most cecal faunal studies have been conducted in domestic fowl, demonstrating the pres-

ence of an abundant population of anaerobic bacteria: $\sim 10^{11}$/g, wet mass, in chickens, but almost as many ($>10^{10}$/g) in other domestic and wild galliforms and ducks (Mead 1989). In chickens, the main bacterial types are anaerobes: gram-positive cocci (28%), gram-negative Bacteroidaceae (20%), gram-positive *Eubacterium* sp. (16%), gram-positive *Bifidobacterium* sp. (9%), budding cocci (6%), *Gemmiger formicilis* (5%), *Clostridium* sp. (5%) and miscellaneous (11%) (Barnes 1972, 1979). Oxygen-tolerant bacteria, yeasts, molds, and protozoa are found in much lower numbers, but it is not surprising that cecal faunas differ from species to species and show a succession of species as the host ages (Mead 1989). Most cecal anaerobes ($\sim 10^9$/g in both domestic and wild birds) can degrade uric acid to volatile fatty acids and ammonia (Mead 1989).

It is well known that avian urine contains uric acid, but contrary to earlier assumptions, it is now known that little of this uric acid has a crystalline structure. Instead, it is in a supersaturated colloidal suspension with Na^+ and K^+ and matrix molecules, forming small (0.5–13 μm) spheres that pass easily through the renal duct system (Braun and Campbell 1989). After reaching the cloaca and refluxing into the lower bowel, these spheres are commonly found in the colonic fecal material, but they are rare in the cecal lumen as a result of their rapid degradation by cecal microbiota (Mortensen and Tindall 1981a, Braun and Campbell 1989). Anaerobic decomposition of uric acid has been reported to yield ammonia, acetate, CO_2, glycine, formate, propionate, complex molecules such as proteins and vitamins, and possibly alcohols; the volatile fatty acids produced are used in or absorbed by the ceca and provide an important energy source (Barnes and Impey 1974, Braun and Campbell 1989). Some of the ammonia released by breakdown of uric acid, urea, and amino acids from both dietary and urinary nitrogenous compounds is used in the production of glutamine and probably other amino acids (Mortensen and Tindall 1981b, Karasawa 1989, Mortensen 1984).

The chemical processes that occur in avian ceca, especially nitrogen cycling and nutrient transport, are still under active investigation. For many years, it was generally held that regardless of what was produced microbially in the cecum, transport across the cecal wall was too poor for the organ to be functionally important. Recent studies (e.g., Moretó and Planas 1989, Obst and Diamond 1989, Thomas and Skadhauge 1989) have shown this to be untrue. For example, using new techniques to measure the nutrient transport capabilities of a wide variety of domestic and wild species—chickens, Rock Doves (*Columba livia*), Canada Geese (*Branta canadensis*), Sage Grouse (*Centrocercus urophasianus*), and Red-necked Phalaropes (*Phalaropus lobatus*)—Obst and Diamond (1989) found cecal transport to exist in all five and to be well developed in most.

Transport varied by cecal region and approached or exceeded intestinal levels in the grouse and phalaropes. Ceca accounted for different amounts of the entire gut's integrated transport capacity: between 0.1% in Rock Doves (with vestigial ceca) and 49% in Sage Grouse (with the largest ceca that occur in tetraonids). Therefore, it is now clear that ceca can contribute in an important way to the nitrogen economy of galliforms and other birds with large functional organs, especially under poor nutritional conditions and other environmental stresses (Dawson and Herd 1983, Björnhag 1989, Braun and Duke 1989, Chaplin 1989).

Disease-causing organisms.—Because they are essentially bags of anaerobic bacteria, protozoa, fungi, and other micro- and macro-organisms, having a relatively constant pH of 6.0–6.5 (Hill 1971), ceca contain both beneficial and disease-causing forms; surprisingly few have been shown to be pathogenic. In addition, there is good evidence that the log-phase growth and subsequent invasion of bacteria such as *Salmonella typhimurium* may be prevented by anaerobes in the ceca (Barnes 1977).

Probably the most notable and pathogenic cecal micro-organism is *Eimeria tenella,* which causes severe bloody coccidiosis in birds, especially domestic fowl. As with many gastrointestinal pathogens, this one can alter cecal motility so that for about two days after infection, the host defecates few of the protozoans and their numbers proliferate. *E. tenella* causes extensive physical damage to cecal tissue (Clarke 1979).

Nematodes (roundworms, pinworms) are the most common macroscopic invaders, moving as swallowed larvae from the upper gut to the colon and into the ceca. Several different species are known to occur in galliforms and anseriforms (Wehr 1965, Watson et al. 1988), with young birds being especially susceptible to heavy nematode infections. The most serious parasitic species in wild birds appears to be *Trichostrongylus tenuis,* which can complete its life cycle without an intermediate host. *T. tenuis* attacks the cecal mucosa, causing anemia, low blood protein levels, increased anorexia, delayed and reduced egg production, and when severe enough, death (Shaw 1990). In northern England and Scotland, this cecal nematode can be devastating to Red Grouse (*L. lagopus scoticus*); individual birds have been reported to carry more than 30,000 worms, although loads of 1000–3000 are more usual in heavily infested areas, and 5000–6000 seem to be fatal (Potts et al. 1984). How strongly this parasite may influence, perhaps even control, the cyclic nature of economically important *L. lagopus* populations in the British Isles is highly controversial (Hudson and Dodson 1990, Cherfas 1990). It should be noted, however, that this nematode does not seriously infest *L. lagopus* throughout the species' range (e.g., Pulliainen 1976).

Other possible cecal functions.—Besides those already discussed, a few other cecal functions have been reported or suggested (McNab 1973).

Significant amounts of vitamins, especially some of the B complex and vitamin B_{12}, were shown to be present in ceca and are probably produced by microbial activity (Couch et al. 1950), but virtually all the work was conducted in chickens. Whether or not cecal vitamin production is important in wild birds is unstudied. Chickens were also believed to be incapable of absorbing vitamins directly through the cecal wall—they had to ingest their cecal droppings if they were to benefit from this vitamin synthesis. In view of recent work on transport efficiency across the cecal wall, this may have been an unwarranted assumption.

Although coprophagy is widespread in parent birds that pick up and swallow the nutrient-rich feces initially produced by their young, few species are known to be coprophagic of adult fecal material. Duke, however, has seen domestic turkeys that were being commercially raised outdoors competing vigorously for and eating cecal droppings (pers. comm.). Wetmore (1926:31) also noted that in an Elegant Crested Tinamou he had just collected "The dung of the adult birds is greenish in color and soft in consistency with a very offensive odor. The crop and alimentary tract of the [downy] chick taken was filled with what was unmistakably the ordure of the parent." From its description, this fecal material was almost surely cecal in origin. It may have served to inoculate the young with important micro-organisms for the uniquely complex ceca found in this species (Fig. 3). It could also have provided the chicks with some other necessary dietary component. Whatever the answer, the presence of cecal feces in the upper gastrointestinal tract of a bird was unusual enough for a long-experienced field biologist to record. In the future, coprophagy may be found to be important in inoculating the ceca of young birds in this, and perhaps other, species (Braun and Duke 1989).

The cecal "tonsil," a visible nodule of lymphoid tissue at the proximal end of chicken ceca, has longer villi than the adjacent tissue and may act as an immunological monitor of luminal contents. The cecal tonsil contains B and T cells and all three classes of the known avian immunoglobulins, IgG, IgM, and IgA (Lebacq-Verheyden et al. 1972, Bienenstock et al. 1973, Glick 1986). Antigen production has also been suggested as a function for glandular ceca and the small ceca that are composed primarily or entirely of lymphatic tissue. This suggestion was made even before the vital immunologic function of the cloacal bursa (bursa of Fabricius) was discovered (Glick et al. 1956). However, subsequent investigations into the avian immunological system have been almost entirely based on chickens, especially when their system was shown to have a strong functional analogy to that of humans (Porter and Parry 1976). Even

the proportions of immunoglobulins in chicken cecal tonsils are not well established: Lebacq-Verheyden et al. (1972, 1974) found a predominance of IgA over IgG, whereas Bienenstock et al. (1973) found just the opposite. Clearly, the immunological contribution of ceca to avian physiology has only partly been elucidated.

Topics on cecal functioning that need to be addressed were outlined by Braun and Duke (1989:127–128) in their concluding remarks after the First International Avian Cecal Symposium. In part, these involved aspects of cecal motility (which we are pursuing), volume and composition of cecal contents, relationships between cecal size and colonic motility and contents, lower gut adaptation after cecectomy, functional cecal differences among species and between adults vs immatures and males vs females of the same species, and cautions about techniques, particularly the potential problems in using domestic birds and insufficient cecal preconditioning before experiments begin. To those remarks, we add:

Although cecal types and sizes have been recorded for many species of birds, the majority remain unreported—gaps in our knowledge that could be filled if more morphologists working with specimens realized the need was there.

When intestinal ceca change their length and/or mass in response to dietary changes, how is that change accomplished? Histological studies are needed.

It will be particularly important for physiologists to explore the functions of ceca that are not of the intestinal type—for instance, how do the large glandular ceca of owls and other birds differ from what is known about the intestinal type? Approximately two-thirds of the birds of the world have small or vestigial ceca that consist mainly of lymph tissue. Because selection pressures have not eliminated these small lymphatic ceca, it is reasonable to assume they have a valuable function. Obst and Diamond (1989) have shown that at least one of these lymphatic types (in the Rock Dove) is capable of transport. Are these small ceca important to a bird's immunological system? Although lymphatic ceca have no obvious special structures like the "tonsils" of galliforms (Klem et al. 1983, 1984), cells in these small ceca may well have similar functions, especially in producing immunoglobulins.

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